for LE plants but not for HE plants. Rough textured leaves have more folds and therefore a greater surface area than smooth leaves of the same length and width. The greater surface area may accommodate a greater number of epiphyll spores, increasing the chance of epiphyll establishment.

Further study should be conducted on the effects of epiphylls on their host leaves. Epiphylls may be detrimental to their host leaves but beneficial to the plant. Epiphylls decrease the amount of light that reaches the leaf and thus decrease photosynthetic activity, but they may enhance nitrogen fixation by providing a suitable habitat for blue-green algae and other nitrogen fixing organisms (Bien 1983). We found that some leaves have characteristics that appear to enhance epiphyll growth. It would be valuable to investigate whether leaf characteristics that enhance epiphyll growth occur more frequently in nitrogen limiting environments.

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THE EFFECTS OF LEAF MORPHOLOGY ON LEAF AREA DAMAGE BY HERBIVORES

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Abstract. (WLO) We examined four aspects of leaf morphology--serration, venation, pubescence, and leaf thickness--and predicted that increasing levels in one or more of these morphological characteristics could influence herbivory between leaves of different species. We found serration and venation to be significantly associated with leaf area damage due to herbivory , while pubescence and thickness did not contribute to protection from herbivory. Undeveloped younger leaves had the same amount of leaf area damage in all species. However, older leaves of different species had different amounts of leaf area damage indicating more highly developed species-specific herbivore defenses in older leaf tissue. Older leaves of all species also had more herbivore damage than younger leaves due to their longer exposure and greater chance of being found and eaten.

INTRODUCTION (SDK)

Insect herbivory has a major influence on the growth and survival of plants. Over time, plants have developed a diverse arsenal of chemical and physical weapons to defend themselves against herbivore attack. Coley (1983) looked at a wide range of physical, chemical, and nutritional plant defenses in many different tropical canopy tree species. Comparing herbivory rates in young and old leaves of pioneer and persistent tree species, she found that young leaves of both life histories experienced the same rate of herbivore damage, while mature pioneer leaves experienced much more damage than mature persistent leaves. Overall, young leaves of all species experienced a higher rate of herbivory than older leaves. Her study further concluded that herbivory was most highly correlated with physical characteristics of leaf toughness, fiber content, and nutritive value. In addition to examining the significant effects of leaf toughness, Coley also found that levels of pubescence were positively correlated with herbivore damage. She concluded, however, that pubescence was spuriously correlated with other more important defense characteristics.

This study examined four aspects of leaf morphology -- serration, venation, pubescence, and leaf thickness -- between young and old leaves of 20 different understory plant species in a Costa Rican cloud forest. We predicted that increasing levels in all four of these traits would deter herbivores. Additionally, the pooled effects of herbivore damage were expected to be greater on older leaves. We predicted that these morphological characteristics could influence differential herbivory between species.

METHODS (WLO)

Twenty species of understory plants, classified by twenty distinct morphotypes, 0.2 - 1.5 m tall were opportunistically sampled from a tropical cloud forest in Monteverde, Costa Rica on 19-20 January 1995. Simple leaves with a range of different morphological characteristics -- serration, venation, pubescence, and thickness -- were selected. Species with compound leaves were not included in this study. Leaves of each species were categorized into specific classes for each morphological trait: 1) serration: large-teeth, small-teeth, or none; 2) venation: basal, linear, primary-superficial, or primary-heavy; and 3) pubescence: smooth, hairy, or very hairy. Five separate plants of each species were sampled along the trail in an understory habitat.

We used leaf area damage as an estimate of herbivore damage, although other disturbances may also cause damage to

leaves. For each plant, we visually estimated the percentage of leaf area damage to the youngest and oldest leaf. Young leaves were those nearest the apical meristem and old leaves were those nearest the bottom of the main plant stem. Newly emerged and dead, shriveling leaves were not counted. If plants exhibited an opposite leaf pattern, we always chose left side leaves for samples.

Visual leaf area estimates were calibrated by drawing the leaf onto graph paper and calculating the percentage of herbivore damage. Using calipers sensitive to 0.05 mm, we estimated leaf thickness of the plant by measuring a middle leaf of average size found between the youngest and oldest leaves on the plant. We also noted the type of herbivore damage (chewing, holes, skeletonization, miners, or galls) done to each individual plant.

RESULTS (SDK)

We found significantly different levels of leaf area damage between the different species (F=1.628, df=19, 180, P=0.54). Young leaves of different species did not experience different amounts of damage (F=1.183, df=19, 80, P=0.293). Old leaves of different species, however, did show significantly different amounts of damage (F=1.802, df=19, 80, P=0.037). Across all species, there was a significantly greater amount of leaf area damage in older leaves

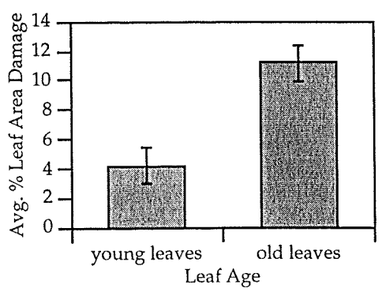

FIG. 1. Average percent leaf area damage (± SE) on young (n=100) and old leaves (n=100). Across all species, older leaves were significantly more damaged than young leaves (see text).

compared to younger leaves (t=-4.377, df=99, P=0.00; Fig. 1).

We tested four different types of leaf morphological characteristics. First, we sampled four species with large serration leaves, four species with small serration leaves, and twelve species with non-serrated leaves. There were significant differences in leaf area damage among leaves with different types of serration (F=4.519, df=2, 197, P=0.012; Fig. 2). Between different serration types, large serration leaves showed significantly more herbivory than non-serrated leaves (P=0.017) and small serration leaves (P=0.022, Tukey means comparison).

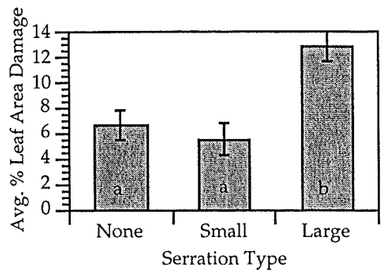

FIG. 2. Average percent leaf area damage (± SE) on leaves with different serration types. Large serration leaves (n=40) showed significantly more damage than small serration (n=40) and non-serrated leaves (n=120). Letters indicate significant differences.

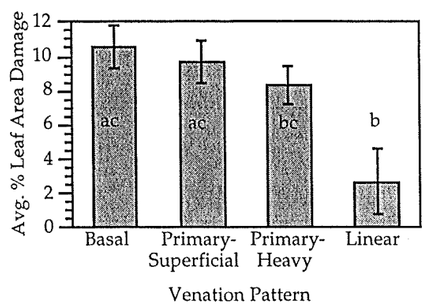

FIG. 3. Average percent leaf area damage (± SE) on leaves with different venation patterns. Basal veined (n=30) and primary-superficially veined leaves (n=60) showed significantly more damage than linear veined (n=50) leaves. Primary-heavy veined leaves n=60. Letters indicate significant differences.

Leaves tested exhibited four different types of venation patterns: basal (3 species sampled), primary-superficial netting (6 species), primary-heavy netting (6 species), and linear (5 species). These differed significantly in leaf area damage (F=4.011, df=3, 196, P=0.008; Fig. 3). Linear venation leaves had significantly less damage than basal venation leaves (P=0.025) and primary-superficial venation leaves (P=0.014, Tukey). Primary-heavy venation leaves did not show significantly more or less damage than any other venation pattern.

We found no significant difference in leaf area damage between leaves with different levels of pubescence based on visual observation: smooth (4 species), hairy (4 species), and very hairy (12 species) (F=0.045, df=2, 197, P=0.956; Fig. 4).

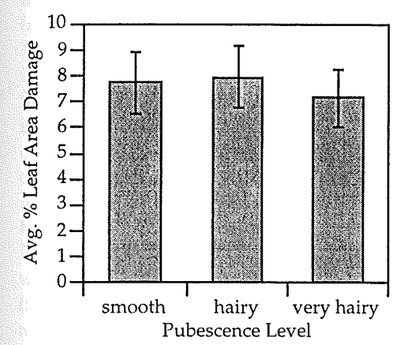

FIG. 4. Average percent leaf area damage (± SE) on leaves with different pubescence levels. Leaves with different pubescence levels did not differ significantly in amounts of damage.

A regression analysis of leaf thickness showed that increasing leaf thickness did not significantly affect the amount of leaf area damage (r^2=0.00, df=1, 198, P=0.724).

Each of the 20 plant species we sampled had experienced some type of herbivore damage. We observed that most leaves showed edge and center chewing, holes, or skeletonization. Only a few leaves (<1%) sampled were infected with galls or miners.

DISCUSSION (WLO)

A considerable amount of herbivory occurs in the understory of tropical cloud forests. Certain morphological traits, such as serration and venation, appeared to differentially deter herbivores more than other traits. We expected leaves with no serration to be most preferred by edge chewing herbivores, while small serrations were predicted to deter these insects. Instead, large serration leaves experienced significantly more herbivore damage than non- or small serration leaves. It seems logical that serration could deter herbivores that feed or chew on leaf edges, yet very few leaves in our samples displayed evidence of edge herbivory and most damage was located in the central portions of the leaves. Because serrations would seem to be useless in protecting leaves from hole boring herbivores, the results probably indicate a spurious association between herbivory and serration. It is likely that other morphological factors are more important in influencing herbivory on these leaves than serration.

Plants with different venation patterns experienced various amounts of herbivory. Assuming that it would be easier for herbivores to burrow and chew leaves with weaker structural designs, we expected herbivores to prefer leaves with fewer, thinner, sparser veins. Thick basal-veined leaves encountered the most herbivory damage followed by primary superficial (thin), primary heavy (thick), and thin, linear veined leaves respectively. Only leaves with linear veins had significantly different level of herbivory. They showed significantly less leaf area damage, supporting our hypothesis that the closely packed pattern of straight, thin veins discouraged insect herbivores.

Surprisingly, we found no difference in leaf area damage among species with different pubescence levels. Very hairy leaves were least affected by herbivory, meeting our original prediction, but there was no significant difference in damage found among the three pubescence levels; this lack of difference suggests that pubescence does not directly influence

herbivore feeding behavior. Although hairs on leaves may deter some herbivores, many insects may be small enough, or conversely large enough, that hairs do not affect their feeding behavior. Along with pubescence, the thickness of leaves did not affect the amount of herbivory damage experienced by these plants.

Older leaves were significantly more damaged by herbivores than young leaves. This is probably explained by the fact that we sampled herbivory at a point of time instead of an herbivory rate over a period of time. Thus older leaves have a greater chance of being eaten due to their longer exposure to herbivory.

Most importantly, the amount of leaf area damage differed significantly among species. Younger leaves of all species showed similar amounts of herbivory while the older leaves showed different amounts of herbivore damage. Our findings agree with Coley's (1983) observations for young leaves and old leaves of pioneer and persistent tree species. It appears that mature leaves have more developed defensive characteristics. With respect to morphology, both young and old leaves of a species share common features of serration and venation, characteristics that did not change with leaf age. Yet young and old leaves experience different levels of herbivory damage, indicating that other changes in nutritive value, chemical compounds, and structural composition occur as leaves age.

Of all the leaf characteristics we examined, leaf age had the most significant affect on leaf area damage. However, this does not imply that leaf morphology has no influence on herbivory among plant species. We did find that serration and venation patterns accounted for some of the differential herbivory observed.

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